# Two new condylarths (Mammalia) from the early Eocene of southern England

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## Synopsis

*Hyopsodus wardi* sp. nov. is described as the first English species of the mainly North American genus *Hyopsodus* and is shown to be closely related to the earliest North American species *H. loomisi*. *Lessnessina packmani* gen. et sp. nov. is described, extending the range of the anisonchine Periptychidae from exclusively the Palaeocene of North America into the early Eocene of Europe.

## Introduction

Collecting over the past two decades in the early Eocene Blackheath Beds of Abbey Wood (London Borough of Bexley) has brought to light a number of mammalian specimens. Amongst these are several jaw fragments and isolated teeth representing two new species of condylarth. One belongs to *Hyopsodus* Leidy, the other to a new monotypic genus. The new *Hyopsodus* specimens have allowed this genus to be recognized in older collections from Abbey Wood and from the Suffolk Pebble Beds (early Eocene) of Kyson, Suffolk, where it had been misidentified. Most previous European records of *Hyopsodus* (Rütimeyer 1892, Teilhard de Chardin & Fraipont 1921) belong to other taxa (see Stehlin 1906 : 632–634; and below). Russell (1968) was the first to record the genus from Europe correctly; Dashzeveg (1977) has described an endemic species from Mongolia.

A relatively small number of mammalian species have already been described from Abbey Wood (White 1931, Cooper 1932*a*, *b*, Simons 1962, Van Valen 1965, Kühne 1969) but recent collecting by bulk sampling, sieving and acetic acid concentration has begun to provide glimpses of a much larger fauna. Remains are sparse and often fragmentary, but the taxa described here are among the best-represented so far. Stratigraphical details of various temporary sections dug in the Blackheath Beds of Abbey Wood appear in Epps & Priest (1933), Rundle (1970; contains numerous additional references), Ward & Cooper (1971) and Hooker (1975). Two lithostratigraphic terms (Lessness Shell Bed and Abbey Wood Member) introduced by Cooper (1976 : 6) are used here but are included in the Blackheath Beds (informal usage) contrary to Cooper's interpretation.

*Material and abbreviations.* Nearly all the specimens described here are in the Department of Palaeontology, British Museum (Natural History); their numbers are prefixed M. Those of other collections are prefixed as follows: University of California (UC); University of Michigan (UM); W. Morris private collection (MC).

The initials of the collectors are indicated where relevant: Messrs S. A. Baldwin, A. G. Davis, F. J. Epps, W. George, P. R. Gurr, J. J. Hooker, R. G. Maynard, A. R. G. Packman and D. J. Ward.

l=maximum length; w=maximum width ($w_1$ and $w_2$ being widths of trigonid and talonid respectively of lower teeth); L=left; R=right.

## Systematic descriptions

### Order **CONDYLARTHRA** Cope, 1881

### Family **HYOPSODONTIDAE** Trouessart, 1879

### Genus ***HYOPSODUS*** Leidy, 1870

TYPE-SPECIES. *Hyopsodus paulus* Leidy, 1870; Bridgerian, Middle Eocene, Wyoming, U.S.A.

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### *Hyopsodus wardi* sp. nov.

Figs 1–6; 8–13

HOLOTYPE. Right maxillary fragment with $P^4$ alveoli and $M^{1-2}$ (M 29762).

PARATYPES. Twenty-four jaw fragments and isolated teeth listed in Table 1.

DERIVATION OF NAME. Named after Mr D. J. Ward, who collected the holotype.

TYPE HORIZON AND LOCALITY. Lessness Shell Bed within the lower sandy Abbey Wood Member of the Blackheath Beds, Sparnacian, early Eocene; the sandpit, Abbey Wood, London Borough of Bexley (National grid TQ 480786).

RANGE. Apart from specimens from the type locality, two isolated teeth of *Hyopsodus* from the Suffolk Pebble Beds of Kyson, Suffolk (TM 269475), may represent this species and are referred to as *H.* cf. *wardi*.

DIAGNOSIS. *Upper molars*: short and broad; ectocingula variably developed; $M^{1-2}$ hypocones small and close to protocones; protostyles present; $M^3$ triangular and without hypocone.

*Lower molars*: short and broad; relatively transverse orientation of opposing buccal and lingual cusps; paraconid prominent and may be isolated from metaconid on $M_1$, small and close to metaconid on $M_2$; talonid notch narrow and with entoconulid; entoconid notch (*sensu* Gingerich & Simons 1977) very shallow.

These characters distinguish *H. wardi* from all described species of *Hyopsodus* except *H. loomisi* McKenna, 1960; this is larger (Fig. 14; Table 1) but morphologically similar, except that it completely lacks upper molar ectocingula. Mean length of *H. wardi* $M^2$ is 2·90 mm.

DESCRIPTION AND COMPARISONS. (Dental terminology follows Van Valen (1966) and Szalay (1969) except that upper mesial and distal cingula are not separated into para- and precingula and meta- and postcingula respectively.)

Size has been shown to be the only reliable character to differentiate contemporaneous species of North American *Hyopsodus* which are otherwise morphologically identical (Gingerich 1976). Morphology in the genus, however, changes with time. Dimensions of the few known upper teeth of *H. wardi* do not overlap with those of the holotype of *H. loomisi*, according to McKenna's (1960 : 106) measurements (see Fig. 14). Those of more extensive assemblages of both species would almost certainly overlap slightly. M 29640, the buccal half of a left $M^1$, assuming that the other three $M^1$s are near the mean, must be close to the upper size limit for *H. wardi*. There is the slight possibility that M 29640 belongs to a larger species of *Hyopsodus* occurring alongside *H. wardi*, but more material is obviously needed to decide this. Apart from the measurements of the holotype, Guthrie (1967 : 38, text-fig. 27) has produced a histogram with measurements of two $M_2$s of *H. loomisi* from Four Mile, Colorado (the type locality), which almost fit within the range of those of *H. wardi* $M_2$s. However, *H.* '*miticulus*' also from Four Mile (see measurements in McKenna, 1960 : table 6) may also refer to *H. loomisi* (personal communication, Dr P. D. Gingerich). If Guthrie's (1967) measurements of *H.* '*miticulus*' from Four Mile are thus included with those of *H. loomisi*, the supposed bimodality not being obvious, the mean $M_2$ length is increased. This mean measure conforms more closely to that expected from the upper tooth measurements of the holotype of *H. loomisi*, and is thus greater than that of *H. wardi*. Gingerich (1976 : text-figs 4–5) has provided statistical measurements of $M_1$ for a sequence of assemblages in the Big Horn Basin, Wyoming, identified as *H. loomisi*, which range fairly widely in size, but would encompass those of the holotype. The stratigraphically lowest of these (1976: text-fig. 5) would overlap considerably with *H. wardi*.

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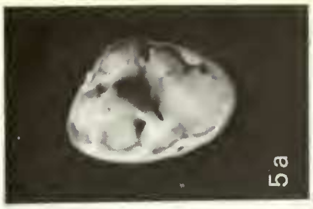
**Figs 1–6.** *Hyopsodus wardi* sp. nov. from the Blackheath Beds of Abbey Wood; upper teeth. Fig. 1, $LP^2$, M 32167. Fig. 2, $RP^3$ (reversed), M 31997. Fig. 3, $LP^4$, MC 44. Fig. 4, **holotype** R maxilla with $P^4$ alveoli and $M^{1-2}$ (reversed), M 29762. Fig. 5, $RM^3$ (reversed), M 29644. Fig. 6, $LdP^3$, M 29745. 'a' suffixes are occlusal views; 'b' suffixes are buccal views.

**Fig. 7.** *Lessnessina packmani* gen. et sp. nov. from the Blackheath Beds of Abbey Wood; $RM^1$, MC 17; a, buccal view; b, occlusal view. All specimens ×6 and sprayed with ammonium chloride.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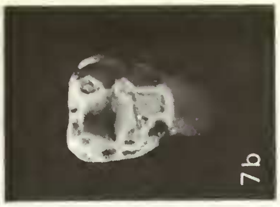
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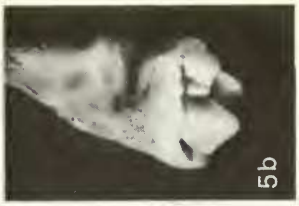
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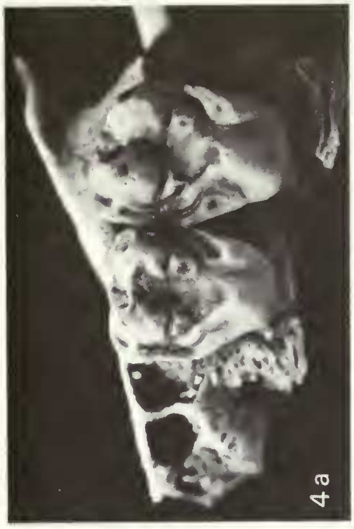
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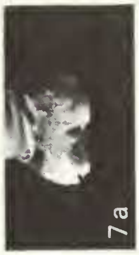
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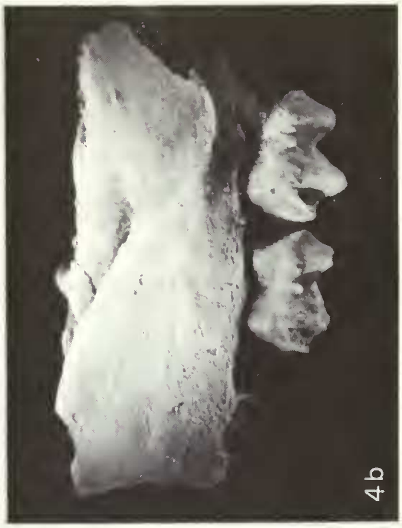
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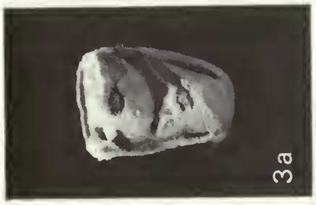
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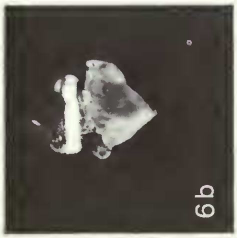
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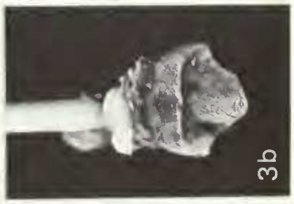
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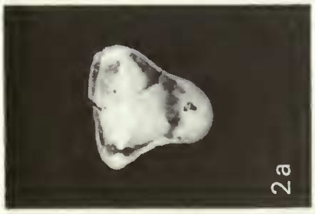
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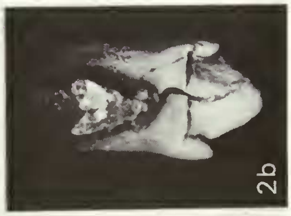
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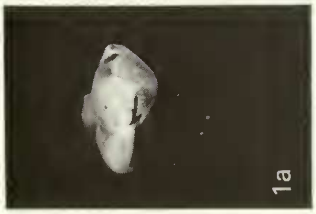
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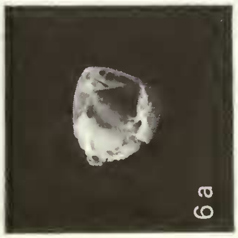
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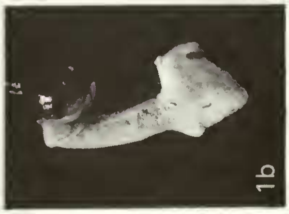
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$P^2$ (M 32167) is almost identical in morphology to that of the holotype of *H. loomisi* (UC 44781; McKenna 1960 : 107, text-fig. 58).

$P^3$ is triangular in outline. M 29408 appears relatively slightly shorter than M 31997, even accepting the broken-off parastyle. The mesiolingual and distolingual margins are slightly concave in M 31997, straight in M 29408. The distal cingulum continues lingually beyond the junction with the postprotocrista in M 29408, but stops at the junction in M 31997. The buccal margin is slightly convex in M 31997, straight in M 29408. M 31997 has a very slight lingual bulge on the postparacrista which suggests an incipient metacone, absent in M 29408. The mesial cingulum in both specimens projects lingually beyond the junction with the preprotocrista. In the holotype of *H. loomisi* the mesial cingulum and preprotocrista form a single crest. In outline shape, of the two Abbey Wood $P^3$s M 29408 is more like the holotype of *H. loomisi*, whilst M 31997 is more like a referred specimen of *H. loomisi* (UM 63620) from Locality 383 of the Bighorn Basin. Thus at least one type of individual variation of *H. loomisi* is paralleled by *H. wardi*.

Of the two $P^4$s, MC 44 is complete and MC 65 is a protoconal fragment. Outline shape of MC 44 is very similar to that of the holotype of *H. loomisi* (UC 44781). Mesial and distal cingula on both have the same lingual extent as in UC 44781. The ectocingulum is complete in MC 44, missing in UC 44781. Presence of a small metacone on MC 44 is suggested by a lingual dentine bulge behind the paracone, unlike UC44781. There is a very small paraconule on MC 44 but not on MC 65. It is missing in McKenna's (1960) figure of UC 44781. The last two features appear to have only individual significance, being variable in different North American *Hyopsodus* species.

The $dP^3$ (M 29745) has a broken mesial edge. It is much smaller than the two $P^3$s, more quadrate in outline, relatively lower-crowned, with a very small metacone and no metastyle. Deciduous premolars of *Hyopsodus* appear to be uncommon in North America. Gazin (1968 : 50; pl. 6, fig. 3) figured the 'best-preserved': $dP^{2-4}$ of *H. lepidus* Matthew, 1909 from the Bridger Formation of the Green River Basin, Wyoming. Compared to $dP^3$ in the figure, M 29745 was apparently less tapered mesially and the distobuccal corner is slightly acute instead of right-angled; the figure is not detailed enough for further comparisons. The size ratios of $dP^3$ to permanent teeth in *H. wardi* are similar to those of *H. lepidus* as shown by Gazin's illustrations (1968 : pl. 6, fig. 3 and pl. 7, fig. 3).

On the upper molars, there is variation in development of the ectocingulum but on the available specimens it is never completely absent as it is on the holotype of *H. loomisi*. McKenna (1960 : 106) used this as a diagnostic character of the latter species. Possible variation in upper molar characters such as development of the hypocone and ectocingulum attributed to *H. loomisi* by Gazin (1962 : 62) refer to assemblages away from the type area of the species and they *may* not be referable to *H. loomisi*. Some of the problems have been discussed by Delson (1971 : 350–351). Most of the upper molars of *H. wardi* have an incipient mesostyle either in the form of a vertical ridge on the buccal wall or a denticle on the ectocingulum. The paraconule and metaconule cristae show much variation in development. There is variation in the buccal saliency of the paraconal region in $M^2$ and $M^3$. $M^3$ varies more than $M^2$ in size, proportions and degree of reduction of the metacone. The distal cingulum on $M^3$ is also variable, in M 29631 there being at its lingual end a minute denticle in the position of a hypocone.

McKenna (1960) could find little significant to write about the lower teeth of *H. loomisi* and did not figure them. For comparison with *H. wardi* I have relied on referred material: a cast of UM 63621 from Locality 383, Bighorn Basin and figures in Gazin (1962 : pl. 9, figs 5–7) of specimens from Bitter Creek, Washakie Basin, Wyoming. The $P_3$s and $P_4$ from Abbey Wood are similar to these teeth in UM 63621 but the trigonids are slightly more open and the paraconids

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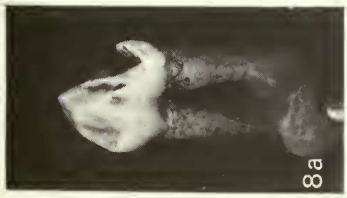
**Figs 8–13.** *Hyopsodus wardi* sp. nov. from the Blackheath Beds of Abbey Wood; lower teeth. Fig. 8, $RP_3$, M 15126. Fig. 9, $RP_4$, M 29757. Fig. 10, $RM_1$, M 15123. Fig. 11, $LM_2$ (reversed), M 29497. Fig. 12, fragment of R mandibular ramus with $M_3$, M 15132. Fig. 13, fragment of R mandibular ramus with $M_{1-2}$, M 15146, in buccal view. 'a' suffixes are lingual views; 'b' suffixes are occlusal views; 'c' suffixes are buccal views. All specimens ×6 and sprayed with ammonium chloride.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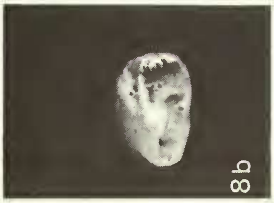
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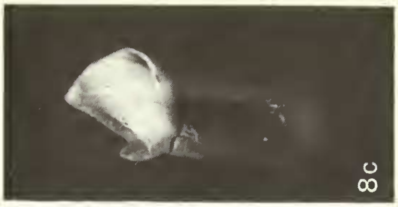
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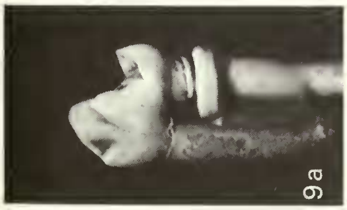
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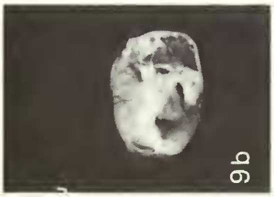
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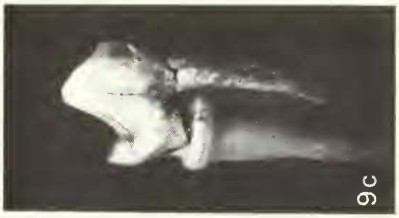
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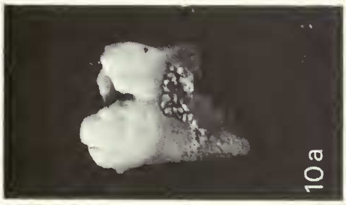
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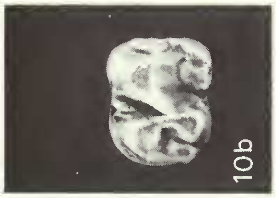
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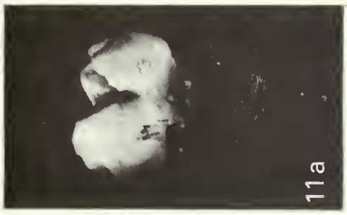
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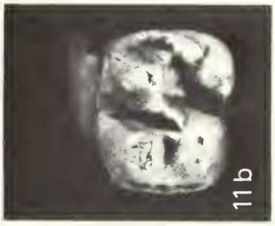
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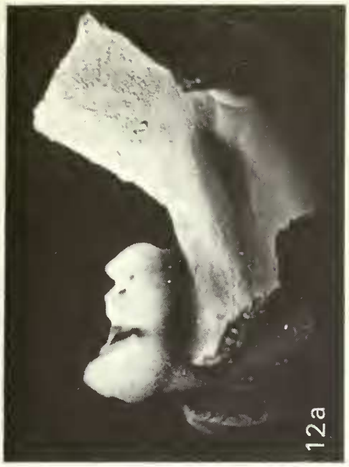
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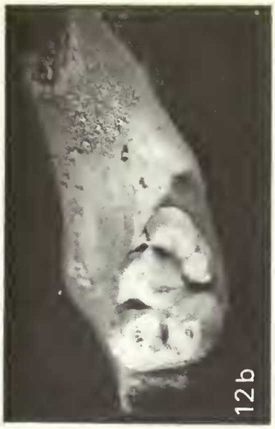
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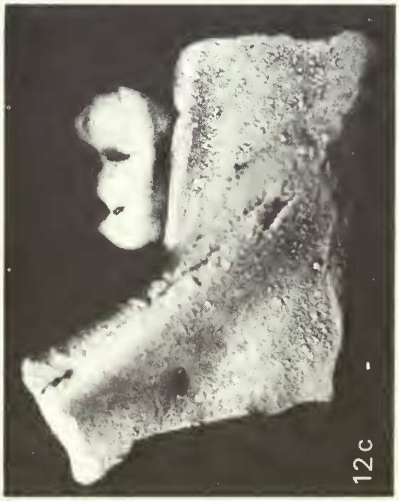
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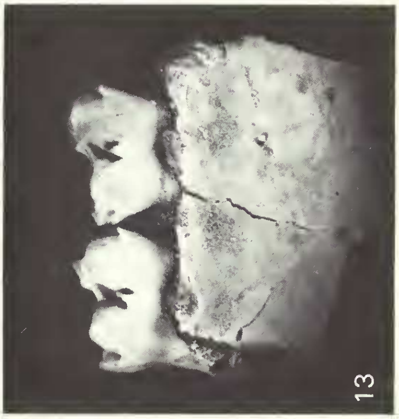
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and metaconids smaller. There is a closer resemblance to one of the Bitter Creek specimens (Gazin 1962 : pl. 9, fig. 6).

*H. wardi* lower molars are very similar to those of UM 63621 and the Bitter Creek specimens except that the crest joining the entoconid and hypoconulid is more prominent, causing these cusps to be less separated (i.e. very shallow entoconid notch). The M$_1$ paraconids seem a little less distinct in the Bitter Creek specimens than in *H. wardi*. Of the two *H. wardi* M$_1$s, one (M 15123) has a distinct paraconid isolated from the metaconid; the other (M 15146), although at a similar wear stage, has a smaller paraconid fused to the metaconid. All the sufficiently well preserved lower molars have entoconulids (= entostylids); some have transversely elongated ectostylids unlike UM 63621. The M$_3$ (M 15132) has a more distally tapering talonid than UM 63621 and, unlike the latter, a buccal cingulum round the protoconid.

Only one specimen of *H. wardi* has M$_1$ and M$_2$ associated. The isolated M 15123 on the one hand and M 29497 and M 29698 on the other can, however, be confidently identified as M$_1$ and M$_2$ respectively. The former has a distinct paraconid and the talonid wider than the trigonid, whilst the latter two have very small paraconids close to the metaconids and talonids equal to or narrower than the trigonids. The other known preultimate molars are too worn or broken to be further identified.

*H. orientalis* Dashzeveg 1977, from the early Eocene of Naran Bulak, Mongolia, has been diagnosed as having M$^2$ significantly larger than M$^3$; hypocone absent on M$^3$; lower molars with well-developed paralophid and weak entoconid from which lingual hypoconulid is weakly separated. The size ratios between some of the M$^1$s and M$^2$s seem more significant than between M$^2$ and M$^3$, but not in every case (judged from Dashzeveg's figures and measurements). In addition, the M$^{1-2}$ centrocristae are acutely buccally flexed, the M$^{1-2}$ parastyles are prominent and, according to the figures, the lower cheek teeth appear higher-crowned than in other *Hyopsodus* species. The M$_1$ paraconid is stated to be present but appears much smaller than in *H. wardi*. Apart from the obvious differences *H. orientalis* is slightly smaller than *H. wardi* although the measurements overlap.

**Table 1.** Length and width measurements (mm to nearest 0·05) of English *Hyopsodus wardi* sp. nov. (including *H.* cf. *wardi*.). Brackets indicate an estimate. Only a single width measurement is given for lower premolars

| Number | Tooth | l. | w. | Number | Tooth | l. | w$_1$ | w$_2$ |
|---|---|---|---|---|---|---|---|---|
| UPPER DENTITION | | | | LOWER DENTITION | | | | |
| M 32167 (RGM) | LP$^2$ | 2·00 | 1·45 | M 15126 (FJE) | RP$_3$ | 2·45 | 1·75 | |
| M 29408 (JJH) | RP$^3$ | – | 2·70 | MC 133 | LP$_3$ | 2·45 | 1·75 | |
| M 31997 (JJH) | RP$^3$ | 2·65 | 2·60 | M 29757 (SAB) | RP$_4$ | 2·75 | 2·00 | |
| MC 44 | LP$^4$ | 2·40 | 3·40 | M 15146 (AGD) | RM$_1$ | 3·05 | 2·30 | (2·45) |
| MC 65 | LP$^4$ | – | – | | RM$_2$ | 3·15 | 2·60 | 2·60 |
| M 29762 (DJW) | RM$^1$ | 2·65 | 3·40 | M 15123 (FJE) | RM$_1$ | 2·85 | 2·20 | 2·30 |
| (holotype) | RM$^2$ | 2·90 | 4·00 | M 29497 (WG) | LM$_2$ | 3·50 | (2·90) | (2·90) |
| M 29631 (ARGP) | LM$^2$ | 2·80 | 4·10 | M 13766 (FJE) | RM$_{1/2}$ | 3·30 | 2·55 | – |
| | LM$^3$ | 2·30 | 3·35 | M 13767 (FJE) | RM$_{1/2}$ | 3·10 | – | – |
| M 20214 (PRG) | LM$^1$ | 2·70 | 3·40 | M 31881 (SAB) | RM$_{1/2}$ | 3·10 | – | – |
| M 29640 (PRG) | LM$^1$ | 3·05 | – | M 15132 (AGD) | RM$_3$ | 3·40 | 2·55 | 2·10 |
| M 29642 (PRG) | LM$^1$ | 2·75 | 3·45 | | | | | |
| M 20218 (PRG) | LM$^2$ | 3·15 | 4·30 | | | | | |
| M 29643 (PRG) | RM$^2$ | 2·90 | 3·90 | M 29698* | RM$_2$ | 3·25 | 2·65 | 2·40 |
| M 29644 (PRG) | RM$^3$ | 2·15 | 3·20 | | | | | |
| M 32144 (JJH) | RM$^3$ | 2·15 | 3·20 | | | | | |
| M 29745 (SAB) | LdP$^3$ | – | 2·05 | | | | | |
| M 29694* | RM$^2$ | 2·90 | 4·45 | | | | | |

**Hyopsodus* cf. *wardi*; not paratypes.

The holotype right maxilla of *H. wardi* is truncated anteriorly at the level of the infraorbital foramen which forms part of the edge. It lies above the former position of the distal half of $P^3$. The orbital floor is preserved with the opening of the maxillary canal above the junction of $P^4$ (now missing) and $M^1$. The base of the zygomatic arch is opposite $M^2$. M 29631 is a left maxilla which shows the base of the zygomatic arch and part of the orbital floor.

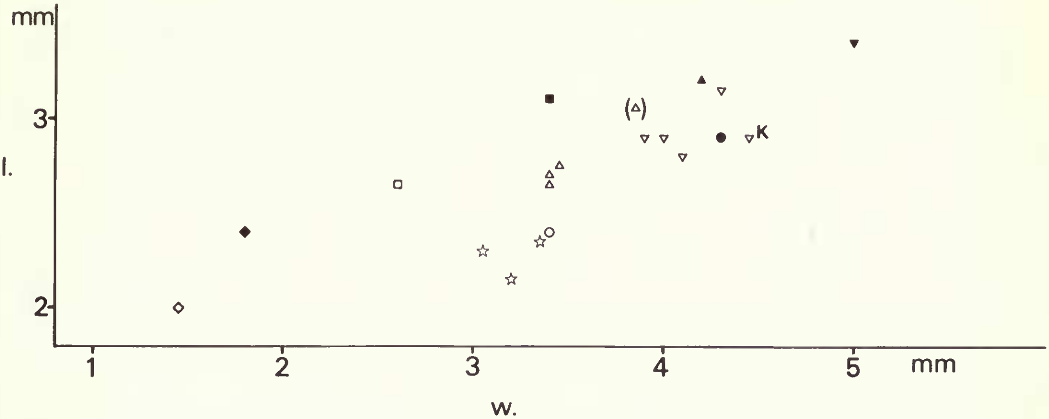

**Fig. 14.** Scatter diagram of length versus width for upper cheek teeth of *Hyopsodus wardi* sp. nov. (hollow symbols) and of the holotype of *H. loomisi* McKenna (after McKenna 1960) (solid symbols). ◇◆ = $P^2$; □■ = $P^3$; ○● = $P^4$; △▲ = $M^1$; ▽▼ = $M^2$; ☆ = $M^3$. K indicates *H.* cf. *wardi* from Kyson. Brackets indicate that the width is estimated.

DISCUSSION. It has been shown above that *H. wardi* is very similar to *H. loomisi*. If North American and English *Hyopsodus* evolved in parallel at the same rate, then the best transatlantic correlation of the Blackheath Beds of Abbey Wood would be with strata in the Rocky Mountains belonging to the Lower Graybullian land mammal age within the early Wasatchian (early Eocene). Savage (1971) pointed out the great similarities between the Sparnacian mammal faunas of north-west Europe and those of the early Wasatchian of Wyoming. He noted that c. 60% of the genera found in Europe were identifiable in North America. This is even more than in the Pleistocene, when glaciations favoured circumpolar ranges, or in the immediately preceding Palaeocene. He suggested that the similarities reflect a sudden migration across the area. In a migration of this kind one would expect even the species to be identical, but this does not appear to be so. This may be because the basal Sparnacian fauna of the Conglomérat de Meudon is poorly known and the main Sparnacian faunas are from higher horizons.

Gingerich (1977 : 63) has pointed out that the European adapid primate *Pelycodus eppsi* (C. F. Cooper) from Abbey Wood differs from all North American *Pelycodus* in that its incipient hypocone arises from the basal cingulum instead of from the postprotocingulum, the difference being the initiation of the subfamily characteristics of the Adapinae and Notharctinae respectively. It would seem therefore that by Abbey Wood times some faunal differentiation, if not also isolation of the two areas, had already taken place. This reduces the reliance one might otherwise place on evolutionary grade in correlating Sparnacian and early Wasatchian faunas. Conversely, any significant time separation of the two faunas would be expected to have produced individual specializations in *H. wardi* as they have in *H. orientalis*. None are apparent in the material at present available, tending to support the correlation suggested above.

*Hyopsodus* is the second most abundantly represented element in the mammal fauna at Abbey Wood. It is surpassed only by *Hyracotherium*, which may reflect a collecting bias caused by past coarse-sieving methods. These were also the two most commonly found genera in the early Wasatchian mammal fauna of Powder River, Wyoming (Delson 1971 : table 1).

The tooth identified tentatively by Teilhard de Chardin & Fraipont (1921) as *Hyopsodus* from the Eocene fissure filling of Vinalmont, Belgium, was dismissed without explanation by Gazin (1968 : 8). From the figure it appears definitely condylarthran, but differs from early Eocene *Hyopsodus* in the following ways. It is more robust; the talonid is higher relative to the trigonid; the paraconid is central instead of lingual; the cristid obliqua trends only slightly mesiolingually and meets the trigonid at a high level; the talonid notch is narrow and shallow; it is much larger.

## Family **PERIPTYCHIDAE** Cope, 1882

### Subfamily **ANISONCHINAE** Osborn & Earle, 1895

### Genus ***LESSNESSINA*** nov.

Type species. *Lessnessina packmani* sp. nov.

Derivation of name. After the type locality in the woods of Lessness Abbey. Feminine.

Diagnosis. Small anisonchine ($P^3$–$M^3$ length 11·0 mm; other measurements in Table 2). $P^3$–$M^3$ protocones large and high and with mesial and distal concavities. $P^{1-2}$ relatively large. $P^{3-4}$ similar to one another, short and broad. Upper molars with low buccal cusps and without ectocingulum. $M^{1-2}$ with well-spaced paracones and metacones; prominent mesostyles; protocones approximately in line with and not buccal to small subequal protostyles and hypocones. $M^3$ reduced.

### ***Lessnessina packmani*** sp. nov.
(Figs 7, 15)

Holotype. Left maxilla with alveoli for canine and $P^1$ and complete $P^3$–$M^3$ (M 29632).

Paratypes (3). Right $P^4$ (M 29756), right $M^1$ (MC 17) and right $M^3$ (M 29637).

Doubtfully referred specimen. Protoconal fragment of a right or left $P^3$ or $P^4$ (M 34648).

Derivation of name. In memory of the late Mr A. R. G. Packman, who collected the excellent holotype.

Type horizon and Locality. Lessness Shell Bed, Abbey Wood Member, Blackheath Beds, Sparnacian, early Eocene; the sandpit, Abbey Wood, London Borough of Bexley (TQ 480786). Known from no other horizon or locality.

Diagnosis. Only known species of the genus.

Description. *Dental formula.* $\frac{?}{?}\ \frac{1}{?\,1}\ \frac{4}{?\,4}\ \frac{3}{?\,3}$. Only $P^2$–$M^3$ are materially known. Two, more mesial single-rooted teeth are represented by alveoli on the holotype. The more distal of these is not separated from either $P^2$ or the more mesial alveolus by diastemata. It once contained a root which was slightly recurved and longer than either of those belonging to $P^2$. The crown would have been broader than and almost as long as that of $P^2$. The remnant distal half of the more mesial alveolus indicates a longer and slightly more recurved root than the first.

These alveoli are considered to have contained the canine and $P^1$, as there is no maxillary/premaxillary suture to indicate that the mesial one is for an incisor, and no interalveolar diastema (i.e. occluding space for a lower canine) to indicate that the distal one is for the upper canine. $P^1$ is normally small in anisonchines (Matthew 1937 : 145–160). Small size of this tooth in mammals is often a prelude to its loss and it could be argued that in a late anisonchine the distal alveolus is more likely to have housed the canine. However, as $P^2$ in *Lessnessina* is somewhat enlarged, it seems more logical to postulate a foward continuation of this trend to explain a large $P^1$.

*State of preservation of the holotype.* The specimen is well-preserved but shows evidence of water transport. The natural edges (i.e. those not broken in collecting) approximately follow the sutural edges of the maxilla, but the convex bone surfaces are slightly worn and the buccal edges

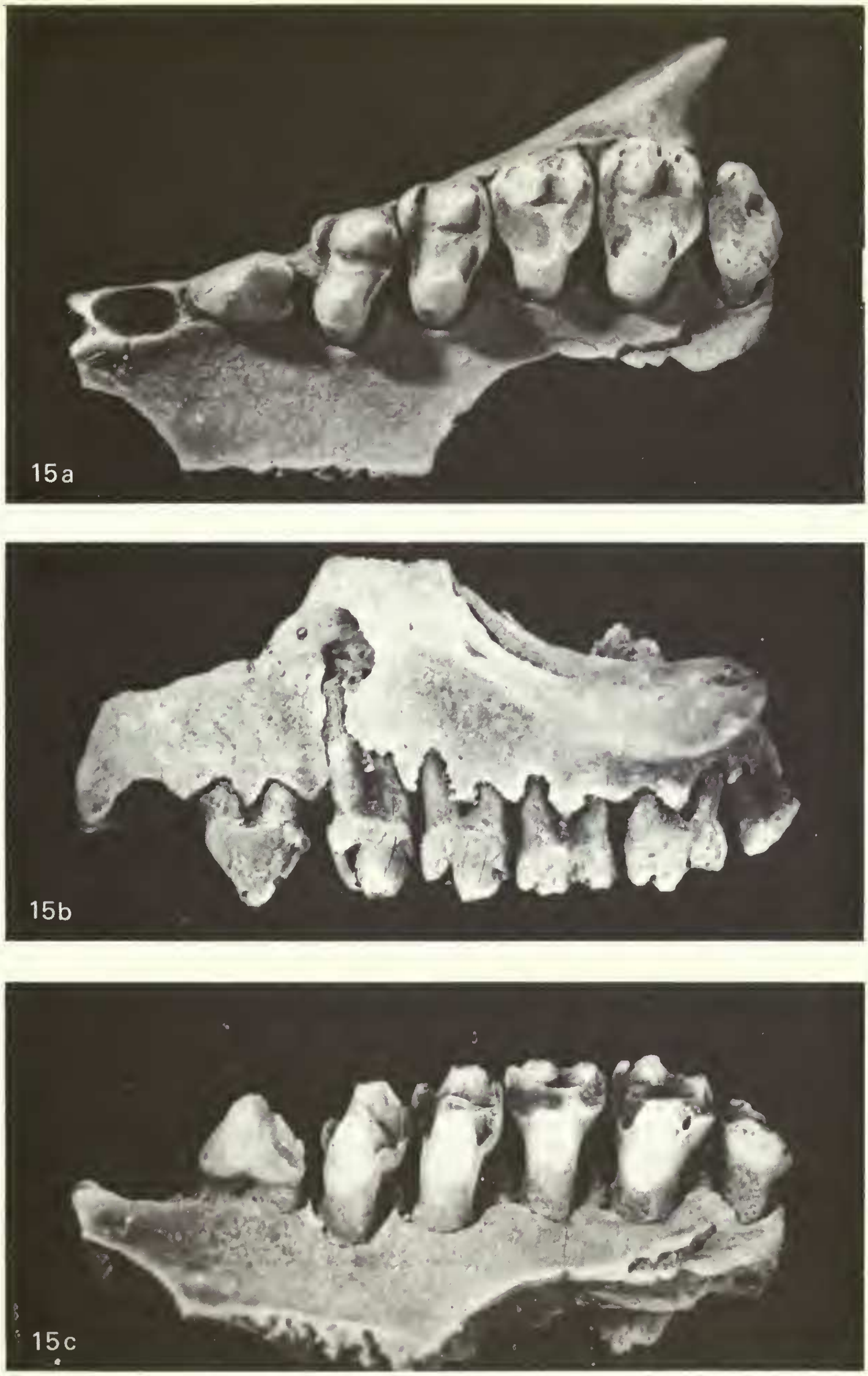

**Fig. 15.** *Lessnessina packmani* gen. et sp. nov. from the Blackheath Beds of Abbey Wood; **holotype** L maxilla with C and $P^1$ alveoli and $P^2$–$M^3$, M 29632; a, occlusal view; b, buccal view; c, lingual view. All views ×6 and sprayed with ammonium chloride.

of the teeth, particularly $P^2$, are somewhat abraded. Natural tooth wear is fairly advanced especially on $M^1$, indicating an old individual. $P^4$ is more worn than $P^3$, which is more worn than $P^2$. This could indicate either a mesially trending eruption sequence, perhaps in response to premolar enlargement in a mesial direction, or a relatively distal area for maximum mastication.

*Upper dentition.* Some of the tooth surfaces are slightly rugose. $P^2$ is long and narrow in outline, broader distally. It is dominated by the paracone. There are large distolingual and steep narrow mesial wear facets. It is separated from $P^3$ by a short diastema. $P^3$ is transversely elongated, with conical paracone and protocone. The parastyle is low but mesially salient. There are rather transverse pre- and postprotocristae, the latter being very weak. The long axis of the tooth is oblique so that the protocone is mesial to the paracone. $P^4$ is almost identical to $P^3$ but the parastyle is higher and extends more lingually; and the postprotocrista is stronger, joining the higher distal cingulum at a small cuspule. It is only slightly larger than $P^3$ in the holotype.

$M^{1-2}$ are triangular in outline and transversely elongated. The lingual half shows a rather sudden narrowing where the large mesial and distal cingula terminate in small protostyle and hypocone. The mesostyle is linked to both paracone and metacone by a low, slightly buccally flexed centrocrista. Although on $M^1$ of both the holotype and MC 17 the paracone and metacone are worn to equal heights, the smaller area of exposed metacone dentine shows that this cusp was lower than the paracone, as can be seen more easily on the other two molars.

The most noticeable feature of the $M^{1-2}$ and to a lesser extent of $P^{3-4}$ and $M^3$ is the shallow convex lingual slope of the protocone whose enamel dives basally below the rest of the crown until it merges without overhang into the massive lingual root.

Wear on $M^1$ of the holotype is deep enough to have fused the protocone, paraconule, metaconule and the large mesial and distal cingula into one large area of dentine, with even a narrow dentinal isthmus extending from the paraconule region to the worn paracone tip. The holotype $M^2$ is less worn and the worn mesial cingulum stands isolated. The paraconule is still fused to the protocone but oddly the metaconule is independent of the protocone but fused to the distal cingulum. From the wear pattern of the holotype $M^1$ it is evident that this tooth also had its protocone and metaconule separated at an earlier wear stage. That this is a variable character is shown by MC 17 where the worn paraconule, protocone and metaconule are fused and independent of the cingula. The upper molar parastyles are strong but merge lingually with the mesial cingulum.

**Table 2.** Length and width measurements (mm to nearest 0·05) of *Lessnessina packmani* gen. et sp. nov.

| Number | Tooth | l. | w. |
|---|---|---|---|
| M 29632 (ARGP) (holotype) | $LP^1$ alveolus | 2·00 | 1·30 |
| | $LP^2$ | 2·50 | 1·65 |
| | $LP^3$ | 2·10 | 2·75 |
| | $LP^4$ | 2·20 | 3·20 |
| | $LM^1$ | 2·45 | 3·30 |
| | $LM^2$ | 2·60 | 3·90 |
| | $LM^3$ | 2·05 | 2·95 |
| M 29756 (SAB) | $RP^4$ | 2·00 | 2·60 |
| MC 17 | $RM^1$ | 2·20 | 2·95 |
| M 29637 (PRG) | $RM^3$ | 1·70 | 2·10 |

The holotype $M^3$ is rather worn and abraded and this tooth is best studied from the smaller paratype (M 29637). The tooth is triangular, tapering distally, with a terminal metacone. The paraconule and especially metaconule are poorly developed. Breakage on both specimens makes it difficult to decide whether or not there was a mesostyle. The distal cingulum curves at its lingual end up the side of the protocone.

*Lower dentition.* Although unknown, this would probably have been similar to that of *Hemithlaeus* except that $M_{1-2}$ would have been relatively longer with more expanded talonids bearing large hypoconids; $M_3$ relatively smaller with reduced hypoconulid but larger hypoconid; $P_{1-2}$ relatively large, $P_2$ a particularly tall tooth according to the long steep mesial wear facet of $P^2$.

*Maxilla.* The palatal process is preserved as far as the midline suture. Part of the lower half of the orbital floor remains and shows the maxillary canal beginning between $P^4$ and $M^1$ and emerging at the infraorbital foramen above the mesial half of $P^3$. The lower orbital margin was formed by the now missing jugal, its contact with the zygomatic process of the maxilla becoming a groove anteriorly. The fact that a portion of orbital rim composed of maxilla occurs anterodorsal to the jugomaxillary suture suggests that the lacrymal was confined to the orbit. The orbit appears to have extended anteriorly to above the junction of $P^3$ or $P^4$. A small elongated foramen occurs near the jugomaxillary suture at the level of $P^4$.

DISCUSSION OF RELATIONSHIPS. *Lessnessina*, the youngest anisonchine, extends the subfamily's upper stratigraphical limit from the Upper Palaeocene to the Lower Eocene and its geographical range from North America to Europe. *Androconus* Quinet, 1965, a supposed periptychid from the Oligocene of Hoogbutsel, Belgium, has been shown to be synonymous with the pantolestid insectivore *Cryptopithecus* Schlosser, 1890 (Heissig 1977).

Because of this considerable range extension, the relationships of *Lessnessina* require some justification. It has the following unspecialized condylarth features. Bunodont cusps, in combination with non-molariform distal premolars; small upper molar hypocones; upper cheek teeth with crowns passing basally into powerful roots without an overhanging lingual enamel edge; absence of $M^{1-2}$ postprotocingulum. One or more of these distinguish it from superficially similar genera in the orders Insectivora such as *Paschatherium* and Primates such as *Plesiadapis*. From the primitive Artiodactyla such as *Diacodexis*, *Lessnessina* differs essentially in its reduced $M^3$ and short transverse $P^3$ as well as in some features which distinguish it also from hyopsodontid condylarths (see below).

Accepting its condylarthran affinities, one sees that the general style of dentition of *Lessnessina* is found only in the Hyopsodontidae and the anisonchine Periptychidae. It has been compared

**Table 3.** Comparative table of characters in *Lessnessina*, Anisonchinae (except *Lessnessina*) and Hyopsodontidae

| Character | *Lessnessina* | Anisonchinae | Hyopsodontidae |
|---|---|---|---|
| $P^3$–$M^3$ length | 11 mm | 16–27 mm | 10–28 mm |
| Nature of cusps | Bunodont | Bunodont | Semibunodont, crests usually more prominent |
| $P^3$ outline | Short, broad, resembling $P^4$ | Short, broad, resembling $P^4$ in *Hemithlaeus* and *Anisonchus* | Triangular, unlike $P^4$ where known |
| Upper molar buccal cusps | Low | High | Low |
| Acute lingual tapering of upper molar outline with enamel extending basolingually | Yes | Yes | No |
| Relative size of $M^1$ metacone | Smaller than paracone | Smaller than paracone | Equal to paracone |
| Relative size of $M^3$ | Reduced | Nearly as large as $M^2$ | Reduced |
| Facial extension of lacrymal | Probably none | Little or none in *Haploconus* (*fide* Matthew 1937 : 159) | Large in *Hyopsodus* |

with original specimens, casts or published figures of the genera contained in these groups, where the upper dentition is known. They comprise the Anisonchinae *Hemithlaeus*, *Conacodon*, *Anisonchus* and *Haploconus* (I follow Van Valen (1967) in referring *Coriphagus* to the Pentacodontidae), and the Hyopsodontidae *Choeroclaenus*, *Mioclaenus*, *Dracoclaenus*, *Protoselene*, *Promioclaenus*, *Ellipsodon*, *Jepsenia*, *Litaletes*, *Hyopsodus*, *Haplomylus*, *Phenacodaptes*, *Apheliscus*, *Aletodon*, *Paratricuspiodon*, *Tricuspiodon*, *Louisina* and *Microhyus* (I follow Van Valen (1967) in referring *Paschatherium* and *Litolestes* to the Adapisoricidae, to which I also tentatively add *Haplaletes* and *Litomylus*).

Table 3 compares key characters of *Lessnessina* with the rest of the Anisonchinae and the Hyopsodontidae. Similarities with the Anisonchinae predominate, particularly the important features of $P^3$ shape, the basolingual enamel extension of the upper molars and the ? non-facial lacrymal. Similarities to the Hyopsodontidae are restricted to rather more generalized characters.

ANCESTRY. Among the known Palaeocene anisonchines, *Lessnessina* is most like the structurally primitive *Hemithlaeus* from the Puercan (early Palaeocene) of New Mexico. *Hemithlaeus* $P^{3-4}$ are, however, somewhat inflated and the parastyles are reduced. *Lessnessina* $P^{3-4}$ are thus more like $P^4$ of the Puercan *Conacodon cophater* (Cope, 1884), but here $P^3$ has lost its protocone. Fundamental morphological similarity is thus closest to a hypothetical latest Cretaceous or earliest Palaeocene common ancestor of *Hemithlaeus* and *Conacodon*, where the premolars have not become inflated, $P^3$ has a protocone and the $M^{1-3}$ hypocones have not enlarged. The evolution of *Lessnessina* from this stage would have involved:

1. ? reduction in overall size
2. reduction of $M^3$
3. enlargement of $P^{1-2}$
4. enlargement of $P^3$–$M^3$ protocones
5. ? expansion of $M_{1-2}$ talonids with enlargement of hypoconids (hypothetical)
6. relative lengthening of upper and probably lower molars
7. acquisition of upper molar mesostyles.

This sequence of events is theoretical as there is no known genus which could be the immediate ancestor of *Lessnessina*. There is a gap of at least 10 million years between the latter and the probable time of its latest common ancestry with the other known anisonchines. The latter all appear to be too specialized to have given rise directly to *Lessnessina*.

Since this paper was submitted I have received from the American Museum of Natural History, through the courtesy of Mr E. Manning, casts of lower dentitions of the hyopsodontid *Oxyacodon*. They are quite dissimilar in detail from those of other hyopsodontids, especially in the structure of the lower molars. The distinct median paraconids (especially $M_{2-3}$), high trigonids and low talonids, prominent entocristids extending to tips of entoconids and metaconids, and mesiolingual cingula, all favour inclusion in the Anisonchinae. *Oxyacodon* lower molar talonids are relatively broader than in other anisonchines, but otherwise cusp pattern is rather similar to that of *Hemithlaeus*. This character is postulated above for the unknown *Lessnessina* lower molars. The reduced *Oxyacodon* $P_{3-4}$ talonids also conform to the morphology expected for *Lessnessina* $P_{3-4}$, from the latter's simple $P^{3-4}$. For a related example, where uppers and lowers are known, compare the occlusal relationships of *Phenacodaptes* $P\frac{4}{4}$. It is possible, therefore, that *Lessnessina* is closer to *Oxyacodon* than to the other anisonchines. *O. agapetillus* (Cope) in particular extends the size range of anisonchines downwards almost to encompass *Lessnessina*.

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